

1 Sex biases in bird and mammal natural
2 history collections

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13 Abstract

14 Natural history specimens are widely used across ecology, evolutionary
15 biology, and conservation. Although biological sex may influence all of
16 these areas, it is often overlooked in large-scale studies using museum
17 specimens. If collections are biased towards one sex, studies may not be
18 representative of the species. Here, we investigate sex ratios in over two
19 million bird and mammal specimen records from five large international
20 museums. We found a slight bias towards males in birds (40% females)
21 and mammals (48% females), but this varied among orders. The
22 proportion of female specimens has not significantly changed in 130 years,
23 but has decreased in species with showy male traits like colourful
24 plumage and horns. Body size had little effect. Male bias was strongest in
25 name-bearing types; only 27% of bird and 39% of mammal types were
26 female. These results imply that previous studies may be impacted by
27 undetected male bias, and vigilance is required when using specimen
28 data, collecting new specimens, and designating types.

29 **Keywords: sex bias, museum specimens, natural history collections,**
30 **birds, mammals**

31 Introduction

32 Museum specimens are used extensively in studies of taxonomy,
33 systematics, biogeography, genomics, comparative anatomy,
34 morphological variability, development, parasitology, stable isotope
35 ecology, toxicology, morphological evolution and more.¹⁻³ They are also

36 of vital importance for understanding how biodiversity responds to
37 anthropogenic impacts.⁴ Large studies of species phenotypes using
38 museum specimens, especially in vertebrates, are becoming increasingly
39 common (e.g. evolutionary dynamics in birds,⁵ ecomorphological
40 diversification in squamates⁶) and are revealing new insights into the
41 evolution of diversity. These studies require large amounts of data, which
42 can mean the focus is on collecting data from as many species as possible,
43 to the detriment of other sources of variation. Sex is an important factor
44 that influences many aspects of an individual's ecology and life-history
45 (Table 1), but it is often treated as a nuisance variable, overlooked entirely,
46 or data collection focuses on just one sex (e.g. only measuring female rates
47 of phenotypic evolution⁷) to avoid the issue. If natural history collections
48 have unbiased sex ratios (i.e. close to 50% males and females, or reflective
49 of the sex ratio for the species in the wild⁸) then this may not be a
50 problem; if there is a bias in the sex composition of collections, this has
51 implications for studies that assume their samples are representative of
52 the whole population or species (Table 1). No large-scale study of sex
53 ratios in bird and mammal museum collections exists, therefore
54 investigating this is of vital importance as the number of studies using
55 museum specimens continues to rise (e.g. this recent special issue on
56 using museum specimens to study biodiversity in the Anthropocene⁴).

Table 1: Prominent uses of natural history specimens and how research outcomes may be influenced by sex biases.

Use	Might sex biases in birds and mammals affect research outcomes?
Taxonomy	Yes. Sexes often have external differences; if these are used in the taxonomy of the group (e.g. male plumage colouration in birds ⁹) then it may be more difficult to identify individuals to species-level in one sex than another. Consistent over-representation of one sex in samples used in taxonomic studies, and in selection of name-bearing types in particular, may mean that interspecific distinctions between taxa are framed most often for that sex, making the less-represented sex harder to identify and distinguish across species, even if important differences exist, a considerable practical problem.

Systematics	<p>Maybe. For standard molecular phylogenies, commonly used genes do not differ substantially among sexes (i.e. not to the extent that they would form different branches). In phylogenomic studies, however, gene trees may vary across a genome if sex chromosomes are included in the sample.¹⁰ Morphological phylogenies are likely to be most affected, as morphological characters can vary extensively between males and females. This also has implications for Total Evidence phylogenies that use both morphological and molecular data. mtDNA is often used to investigate species limits (e.g. gentes limits in cuckoos¹¹) and this may differ across sexes.</p>
Biogeography	<p>Maybe. This depends on the scale at which you consider biogeography. In species where all reproduction is sexual, sexes (necessarily) do not differ in terms of large-scale historical biogeography, i.e. colonisation of new regions will not succeed if only one sex colonises. However, locally sexes may be spatially segregated (e.g. bat roosting sites¹²), and have different dispersal rates¹³ or patterns of habitat use, and differential migration of sexes is common in birds.¹⁴</p>

Genomics	Yes. Mammals and birds have chromosomal sex determination; in mammals XY male and XX female, in birds ZZ male and ZW female. ¹⁵ The X and Z chromosomes are larger and have more genes than W and Y, thus genome size differs among sexes. Many genes are also sex-linked, so genomes will differ between sexes.
Comparative anatomy	Yes. Males and females have internal and external anatomical differences, thus sex biases will influence comparative anatomy studies.
Development	Maybe. In most vertebrates, early developmental stages are almost identical in males and females, however later development and sexual maturation involve highly divergent growth to result in adult sex differences. ¹⁶ If research is focused on early development or juvenile life-history stages then sex biases are unlikely to pose a problem.
Morphological variability	Maybe. Perceived wisdom is that males are more variable than females. However, many detailed morphometric studies do not find this (e.g. in mammalian dentition and skull variation ^{17,18} and references within) in birds or mammals when a large sample is included. In some groups females are more variable than males (e.g. in <i>Pyriglena</i> antbirds ¹⁹).

Parasitology	Yes. Males are commonly more susceptible to infection, have lower immune function, and higher parasite loads than females. ²⁰ This is likely due to testosterone inhibiting the immune system. ²¹ However, this is not true for all species and all kinds of parasites, e.g. breeding female birds have more blood parasites than males. ²² Differences in either direction may cause parasite load and diversity to be misrepresented where collections are sex biased.
Stable isotope ecology	Yes. The demands of producing eggs, brooding, pregnancy, and lactation can alter stable isotope ratios. ²³ Many species also have sex segregated diets, e.g. leopards, ²⁴ and foraging ranges, so stable isotope ratios may vary among sexes even in non-breeding individuals.
Toxicology	Yes. As above, sexes may differ in foraging ecology, which has consequences for contaminant burden. Furthermore, females may be able to eliminate some contaminants via eggs (e.g. mercury ²⁵), an option not available to males.
Morphological evolution	Yes. There is extensive sexual dimorphism in many of the traits used in studies of morphological evolution, for example body size, ²⁶ thus tempo and mode of evolution may vary with sex.

57 Here we investigate sex biases in natural history collections of birds and
58 mammals using over two million specimen records from five major
59 international museums. We find a slight bias towards males in both
60 groups. Curators and collections managers do not as a rule discard
61 specimens based on sex, thus any bias is likely related to what is collected
62 in the field. Male bias may be related to active selection for males by
63 collectors in the field, or active avoidance of females with young due to
64 legislation, ethical or conservation considerations. In particular a major
65 suspected source of male bias in collections for some species is deliberate
66 selection for large, “impressive” male specimens, especially where males
67 are larger or more colourful than females, or possess ornaments or
68 weaponry such as horns or antlers. Given the age of most major natural
69 history collections, some male bias may be related to the changes in
70 attitudes towards sex through time, therefore, we expect male bias to
71 decrease towards the present due to changes in collection methods and
72 motivations over the last century. Alternatively, male bias may be
73 accidental, for example due to trapping biases (i.e. trapping method,
74 season of collecting, conspicuous male behaviors or traits), difficulties
75 identifying females to species-level, or in some cases simply because there
76 were more males in a population. In some mammals, higher dispersal,
77 and broader habitat use, in males may result in them being more likely to
78 come into contact with hunters or traps; males may also exhibit lower
79 levels of neophobia increasing their likelihood of being captured, though
80 evidence for this is limited.^{27, 28} In some birds, male territorial calls are
81 often used to bring individuals towards a trap, which may also bias
82 collections towards males.

83 To investigate these biases further, we tested whether male bias differed
84 among orders, with sexual size dimorphism, with the possession of
85 colourful plumage (birds) or ornamentation or weaponry (mammals) in
86 males, and through time. Note that these variables mostly test for
87 deliberate selection for males, because these data are easier to collate, but
88 our results are likely a combination of deliberate and accidental male
89 biased collecting.

90 **Materials and Methods**

91 **Data collection and cleaning**

92 **Specimen data**

93 We obtained museum bird and mammal collection records from the
94 Global Biodiversity Information Facility (GBIF²⁹). Specifically we collated
95 data from the American Museum of Natural History (AMNH;
96 $n = 271,407$ records^{30,31}), Field Museum of Natural History (FMNH;
97 $n = 182,984$ records^{32,33}), Muséum National d'Histoire Naturelle
98 (MNHN; $n = 86,126$ records^{34,35}), National Museum of Natural History,
99 Smithsonian Institution (NMNH; $n = 496,735$ records³⁶), and Natural
100 History Museum, London (NHMUK; $n = 251,409$ ³⁷). These specimens
101 were obtained between 1751 and 2018, mostly through hunting or
102 trapping, and sexed based on internal or external genitalia or secondary
103 sexual characters, for example plumage colouration or antlers. All raw
104 data can be downloaded from GBIF.²⁹

105 Prior to analyses we cleaned the data as follows. (i) Record type. To avoid
106 confusing specimens with archives describing specimens we selected only
107 preserved specimen records; (ii) Age. Juveniles can be harder to sex so we
108 excluded all juveniles, young and foetuses from the dataset; (iii) Year. We
109 removed collection years later than 2018 as these were clearly errors; (iv)
110 Taxonomy. We removed subspecies names and used species binomials
111 because we were interested in species-level sex ratios. To ensure our
112 results were not due to female specimens more frequently being identified
113 to the genus-level only, we also also created a dataset with all specimens
114 with valid generic names. We corrected bird taxonomy using the GBIF
115 backbone taxonomy,²⁹ and mammal taxonomy using Mammal Species of
116 the World;³⁸ (v) Type status. We split types into name bearing (Holotype,
117 Syntype, Lectotype, Neotype) and non-name bearing (all others) types.
118 Where the records did not specify the kind of type we define these as
119 ambiguous types; (vi) Sex. We standardized sex to either Female, Male or
120 non-sexed, and removed intersex or hermaphrodite individuals. Note that
121 we recognise that biological sex is a spectrum.³⁹ We focus here on
122 specimens identified as females and males for simplicity because there
123 were very few recorded intersex specimens in collections databases (only
124 five remained after other data cleaning), but we recognize the importance
125 of these individuals. We also excluded non-sexed individuals from the
126 analyses. The final dataset contained 2,496,611 specimens (1,395,748 birds
127 and 1,100,863 mammals), 1,647,409 (708,355 birds and 939,054 mammals)
128 of which were sexed (Table A1).

Sexual dimorphism, plumage colouration and ornamentation data.

We extracted median body masses (g) for males and females from Lislevand et al.⁴⁰ for birds and Jones et al.⁴¹ for mammals, then calculated sexual size dimorphism by dividing mean male body mass by female body mass. Note that the sample size for these variables is lower because sex disaggregated body size data are rare (see Table A2).

To explore how “showiness” might influence sex bias, we included a measure of plumage colouration for passerine birds taken from Dale et al.^{42,43} This measure is based on the mean RGB (red green blue) values for 400 randomly chosen pixels in six patches (nape, crown, forehead, throat, upper breast, and lower breast) for each sex. We then calculated a plumage dimorphism score by dividing male plumage score by female score for each species. For mammals, we used the Handbook of Mammals of the World to identify mammals where males have “ornamentation”. We defined ornamentation as a feature that might increase the likelihood of a collector targeting an individual, specifically horns, antlers, tusks, well-defined manes (i.e. in lions and some baboons), enlarged nasal appendages (e.g. in elephant seals, proboscis monkeys and hammerhead bats), facial colouration (e.g. in mandrills) or large cheek extensions (e.g. orangutans). Where species had ornaments, we recorded whether both sexes or only males routinely possess them. Note that the majority of species with ornaments in our models were Artiodactyla (59 of 67 species).

Bird species in several groups show reverse sexual dimorphism, where females are larger or showier than the males. To see if we detect a different pattern in these species we also divided the bird data into species where

154 the female is generally the larger or showier sex (the families Accipitridae,
155 Falconidae, Scolopacidae, Charadriidae, Jacanidae, Stercorariidae, Sulidae,
156 Fregatidae, Cuculidae, Trochilidae, Pipridae, and the orders Strigiformes
157 and Struthioniformes - list taken from⁴⁴), and species where the male is
158 generally the larger or showier sex (all other species).

159 The final cleaned data are available on the NHM Data Portal.⁴⁵

160 **Analyses**

161 We analysed bird and mammal data separately and performed all
162 analyses in R version 3.5.0.⁴⁶ Reproducible scripts are available on GitHub
163 at <https://github.com/nhcooper123/sex-bias-museums>.⁴⁷

164 We first summarised the overall proportion of female, male and unsexed
165 specimens, and calculated the median proportion of females across
166 species (using the main species-level dataset) and genera (using the
167 generic-level dataset). We then summarised differences in the proportion
168 of female specimens across orders and types.

169 Unsexed specimens may bias our results toward males if the majority of
170 unsexed specimens are female. We tested for this by fitting linear models
171 to compare the percentage of unsexed specimens and the percentage of
172 female specimens within species; if these unsexed specimens are generally
173 female we expect to see a negative relationship between unsexed
174 specimens and the proportion of females in a species. In addition, we
175 investigated variation in the numbers of unsexed specimens by order,
176 collection continent and collection decade (see Supplementary Materials).

177 Most species were represented by only a few specimens (Figure A1), with
178 large skews towards either males or females at low numbers (Figure A2).
179 To reduce problems this is likely to cause when fitting models, we used
180 only species with 100 or more specimens in our models (see
181 Supplementary Materials for more details), except in our change through
182 time models. In these models our response variable was the proportion of
183 males and females in each species for each year from 1880-2010 (before
184 1880 and after 2010 we did not have any species with sufficient specimens
185 to include). As there were only 55 bird species and 1,216 mammal species
186 with over 100 specimens in a year, change through time models instead
187 used all species with more than 50 specimens in a single year to increase
188 the sample size (see Table A2).

189 We fitted all models using generalised linear models (GLM) with
190 quasibinomial errors, with the proportion of female specimens (success)
191 and the proportion of male specimens (failure) for each species as the
192 response variable (i.e. a binomial response where the number of females
193 and the number of males for each species were jointly modeled).
194 Quasibinomial rather than binomial errors were used due to
195 overdispersion (all models have deviance/residual degrees of freedom far
196 greater than two; see output on GitHub for exact values), and we assessed
197 the significance of model terms using Type II sums of squares. We used
198 standard model checks for GLMs (Q-Q plot, histogram of residuals,
199 residuals vs. linear predictors, response vs. fitted values) to assess model
200 fit. We tested whether the proportion of female and male specimens
201 varied with (i) orders; (ii) collection years (1880-2010); (iii) male body
202 mass (log transformed); (iv) sexual size dimorphism (log transformed); (v)

203 whether males were larger/more showy than females or vice versa
204 (reverse sexual dimorphism; birds only); (vi) plumage dimorphism (log
205 transformed; passerine birds only); and (vii) ornamentation (mammals
206 only). The number of specimens and species in each model are shown in
207 Table A2.

208 **Results and Discussion**

209 Of the 2,496,328 specimen records (1,395,748 birds and 1,100,580
210 mammals) in our dataset, 20% of bird specimens were female, 31% were
211 male, and 49% were not sexed (Table A1). For mammals, the number of
212 non-sexed individuals was much lower at 15%, likely because it is often
213 easier to identify sex in mammals, with 41% female and 44% male
214 specimens. If we consider only sexed specimens, 40% of bird and 48% of
215 mammal specimens were female (Figure A3). In real terms this represents
216 143,905 more male than female specimens in birds and 40,468 more male
217 specimens in mammals. This male bias was not due to unsexed specimens
218 mostly being female (see Supplementary Materials; Figures A4-A8).
219 Results were also qualitatively similar using the generic-level data (Table
220 A1), so we focus only on species-level data below.

221 In the wild, adult sex ratios in many bird species are male skewed, though
222 on average not as skewed as our results ($n = 187$ species, median 44.8%
223 female;⁴⁸ see Supplementary Materials; Figure A9), however, 48% is not a
224 large deviation from the 50% expected in many natural populations of
225 mammals.⁸ Well sampled species (i.e. those with at least 100 specimens)
226 with the most extreme sex ratios in our data, i.e. species with fewer than

227 25% female or 25% male specimens, are shown in Table A3.

228 **Variation among orders.**

229 The proportion of female specimens varied across orders for both birds
230 ($F_{24,1721} = 29.81$, $p < 0.001$; Figure 1; Figure A10; Table A4) and mammals
231 ($F_{24,1488} = 19.80$, $p < 0.001$; Figure 2; Figure A11; Table A4). Most orders
232 had more males than females (Table A4). In birds, of the 25 orders with
233 sufficient data, only tinamous (Tinamiformes; 50.4%) had more females,
234 but these represented just four species in the dataset. The most
235 male-biased orders with more than 25 species were pigeons and doves
236 (Columbiformes; 36.8% female), hummingbirds and swifts (Apodiformes;
237 37.2%; but see Supplementary Materials; Figure A12), and passerines
238 (Passeriformes; 38.4%). Adult sex ratios in Columbiformes and
239 Passeriformes are generally male-skewed,^{48–50} but hummingbirds are
240 often female-skewed in the wild.^{48,50} This, along with evidence that, on
241 average, Passeriformes are not as male biased as our results ($n = 54$
242 species, median 45.1% female⁴⁸), suggests that greater availability of males
243 alone cannot account for our results.

244 Seven of the 25 mammalian orders with sufficient data had more females,
245 the most extreme being anteaters and sloths (Pilosa; 71.1% female). Most
246 mammal species have a sex ratio of 1:1 at birth,⁸ though this can vary in
247 adults. Several species of sloth have higher numbers of females (up to
248 68.8% females⁵¹) which may explain why we also found more females in
249 collections, however, giant anteaters (*Myrmecophaga tridactyla*) show
250 variable sex ratios in the field,⁵² but strong female bias in collections

(71.3% female). Among the orders represented by more than 25 species in our data, only bats have more females (Chiroptera; 52.2% female; Figure 2), despite reportedly balanced adult sex ratios in the wild.¹² This is likely related to widespread sex segregation in bat roosting sites, with many roosts containing individuals of only one sex.¹² In the the past, bats were often trapped by collecting all individuals in a roost site, and female bats may use fewer roost sites than males (e.g. in *Myotis daubentonii*⁵³), so skew towards females is not surprising. The most male-biased order of mammals were the even-toed ungulates (Artiodactyla; 39.7% females), but although they exhibit a great deal of variation in adult sex ratio, on average, there are more females than males in wild populations⁵⁴ suggesting strong selection for male specimens in this order derived from the deliberate hunting of large males that was common in the 19th and early 20th centuries.

Changes through time.

We found male bias increased for birds ($F_{1,389} = 7.167$, $p = 0.008$; Figure A13), but decreased for mammals ($F_{1,3426} = 6.86$, $p = 0.009$; Figure A13), however the effect sizes were extremely small (birds: $slope \pm SE = -0.002 \pm < 0.001$; mammals: $slope \pm SE = 0.001 \pm < 0.001$), indicating very little change in either class, i.e. there has been no improvement in the sex balance of collecting over the last 130 years.

Male body mass and sexual size dimorphism.

We found significant effects of male body size on the proportion of female specimens in both birds and mammals (Table A5), however, the direction and strength of the relationship varied among classes and orders (Figures A14-A16; Table A5). Bird species with larger males tended to have more female specimens, whereas the reverse was true for mammals. In mammals this was likely driven by a few orders with large males that have long been favored in collections (e.g. Artiodactyla, Carnivora) and have low median percentages of female specimens (Figure 2; Table A4). Interestingly however, selection for males in these groups did not increase with increasing male body size (Figure A16), instead it appears male carnivores and artiodactyls were preferred over females, regardless of their body size.

Rather than selecting large males *per se*, collectors may favour males when the difference in size between females and males, i.e. sexual size dimorphism, is large. We found that as sexual size dimorphism increased, i.e. as males became increasingly larger than females, there was more bias towards male specimens (Table A5), however, this result was entirely driven by differences among orders (Figures A17-A18); when order was included in the models, sexual size dimorphism did not significantly influence specimen sex ratios over the effects of order (Table A5). As with body mass, this suggested certain orders were more likely to contain more male specimens, regardless of their size with respect to females, suggesting that other characteristics were driving their selection.

In birds that show reverse sexual dimorphism we found that the median

percentage of females for species where the male was the larger or showier sex was 40%, the same as for the whole dataset. For species where the female is the larger or showier sex the median percentage of females was 44.6%, closer to the expected 50:50 ratio. There were significantly more females in species where the female is the larger or showier sex ($F_{1,1744} = 167.9$, $p < 0.001$; Figure A19).

Plumage and ornaments.

In passerine birds, as males became increasingly more colourful than females, the proportion of female specimens decreased (Figure 3; $F_{1,828} = 58.95$, $p < 0.001$; $slope \pm SE = -0.416 \pm 0.054$). This relationship was not strong, but fits with anecdotal evidence of collectors preferentially selecting colourful male specimens, especially where plumage differences are large, for example in birds of paradise. Although the numbers are too small to drive the differences seen here, there is also bias towards displaying male specimens in exhibits.⁵⁵

For mammals, species with ornaments (horns, antlers, tusks, manes etc.) had significantly fewer female specimens than those without ornaments (Figure 4; $F_{1,1510} = 46.98$, $p < 0.001$; $slope \pm SE = -0.328 \pm 0.048$). Note, however, that only 67 species across four orders in our analyses had ornamentation (Table A6). Most of the species with ornaments in our models were artiodactyls, and most artiodactyls have horns, antlers or tusks, suggesting that the strong male bias in Artiodactyla (39.7% female; Figure 2) was due to selection for males with these features. Within ornamented species there was no significant difference if both sexes or

only males possessed the ornament (Figure 4; $F_{1,65} = 0.725$, $p = 0.398$), suggesting that even where females are phenotypically different, preference is still given to collecting males. This is particularly concerning since most artiodactyl species are female skewed in the wild.⁵⁴ We note, however, that artiodactyls only make up 4% of our dataset, and just over 4% of all mammal species,³⁸ so while deliberate hunting of large males may be a driver in this order, it is unlikely to drive all male biases we see.

Type specimens.

Perhaps our most notable finding focused on name bearing type specimens (holotypes, syntypes, lectotypes, and neotypes). Here the bias towards male specimens was extreme; only 25% of bird and 39% of mammal types were female (Figure A3). Although in some instances, males might be considered the appropriate sex for holotypes because male characters such as plumage or bacula are diagnostic (e.g. in bats⁵⁶), we see no reason to not also designate a female paratype to represent the phenotypic range of a species - with the exception that in rare species, or species with few specimens for another reason, this may not be possible. In mammals paratypes were almost 49% female, but bird paratypes were 38% female. Additionally, for newly discovered species, genetic identification of species limits may remove the need for male diagnostic characteristics, and thus male holotypes. Currently sex does not form any part of the International Code for Zoological Nomenclature (ICZN) recommendations for designating types, although some historical instructions for collectors emphasize the importance of multiple types (e.g. the classical description of the type⁵⁷). Adding this to the ICZN is of

346 vital importance moving forwards.

347 **Conclusions and recommendations.**

348 Here we tested for deliberate selection of large, showy males, especially in
349 species with high levels of sexual dimorphism in these traits. Our
350 analyses suggest that some male bias in collections is the likely result of
351 historical active selection of males. In mammals, males are favoured in
352 species with larger males, and in species with ornaments. These results,
353 however, are driven by carnivores and artiodactyls, and do not account for
354 male biases in species which are not actively targeted by hunters, for
355 example most rodents. In birds, showier males appear to be favoured
356 within passerines, and species that exhibit reverse sexual size dimorphism
357 show less bias towards males. As passerines make up 58% of our dataset
358 (and around 60% of all bird species), active selection for males may be a
359 much larger problem in birds than in mammals. To reduce these
360 imbalances, collectors in the field should strive to avoid trapping biases
361 and biases in selecting individuals to collect.

362 Much bias towards males is probably non deliberate, and related to the
363 characteristics of individual species and how they are trapped. In small
364 mammals, for example, higher dispersal and broader habitat use in males
365 may result in males being more likely to come into contact with hunters
366 or traps.¹³ In passerines, male calls are often used to draw birds towards a
367 mist net, resulting in higher numbers of males being trapped (a simple
368 solution to this is to also use playback of female calls, an active area of
369 current research in ornithology⁵⁸). Some trapping is also opportunistic, so

characteristics that mean one sex is exposed to collectors more often may play a key role. For example, the slight female bias in Tinamiformes (50.4%) in this study may be because they are often collected on their nests. Similar patterns are likely for other conspicuous ground-nesting birds. Differential migration of sexes may also influence the numbers of males and females caught at certain locations throughout the year.¹⁴ More ecological studies on species with strong biases towards males or females are needed to help explain these patterns. On top of these factors, females may be harder to identify than males - they may appear similar to juveniles, or lack diagnostic features such as bacula that make identification simpler. If this is the case, many of our unsexed specimens may be female. Our supplemental analyses (Figures A4-A8) suggest this does not cause the male bias, but until these 687,393 unsexed bird and 161,526 unsexed mammal specimens are sexed, we cannot determine it would have no effect.

Museum professionals, and those using museum collections, should have an awareness of the biases within their collections (not just in terms of sex but also in terms of age, locality, and other factors), and attempt to acquire material to best resolve those biases, whatever their cause. Natural history collections play a critical role in informing multiple research disciplines answering vital questions for the future of biodiversity⁴ and are also key resources for public engagement and interaction with biodiversity.⁵⁵ Therefore it is paramount that we continue developing these resources while using a more comprehensive and better informed approach. Finally, researchers investigating broad-scale variation in species should account for these biases when designing data collection protocols and/or in

396 downstream analyses and declare how they dealt with those biases in
397 resulting publications. Our analyses place particular pressure on
398 taxonomists to think more carefully about sex when defining
399 name-bearing types, and suggest more designation of opposite sex
400 paratypes would be desirable, particularly in birds.

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403 two anonymous reviewers for insightful comments on an earlier version.

404 **Data accessibility**

405 Data are available from the NHM Data Portal⁴⁵ and GBIF.²⁹ R code is
406 available from GitHub
407 (<https://github.com/nhcooper123/sex-bias-museums>; Zenodo DOI:
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Author contributions

NC performed the analyses and wrote the first draft. All authors contributed to study design, interpreted results, revised the manuscript, and approved the submitted version.

Competing interests

The authors declare no competing interests.

Figures

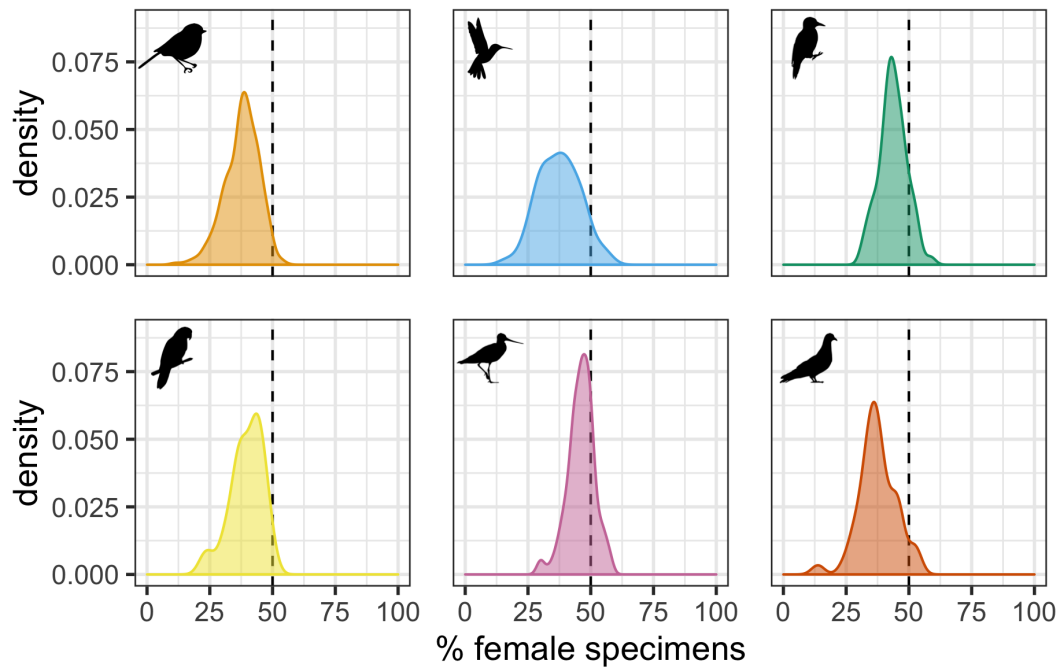


Figure 1: Kernel density plots showing the % female specimens in each species across the six largest orders of birds (from left to right, top to bottom: Passeriformes, Apodiformes, Piciformes, Psittaciformes, Charadriiformes, and Columbiformes). Only species with at least 100 specimens are included. The dashed line represents 50% female specimens. Silhouettes are from PhyloPic.org contributed by Ferran Sayol (parrot, hummingbird, tit), Steven Traver (woodpecker) and Alexandre Vong (shorebird).

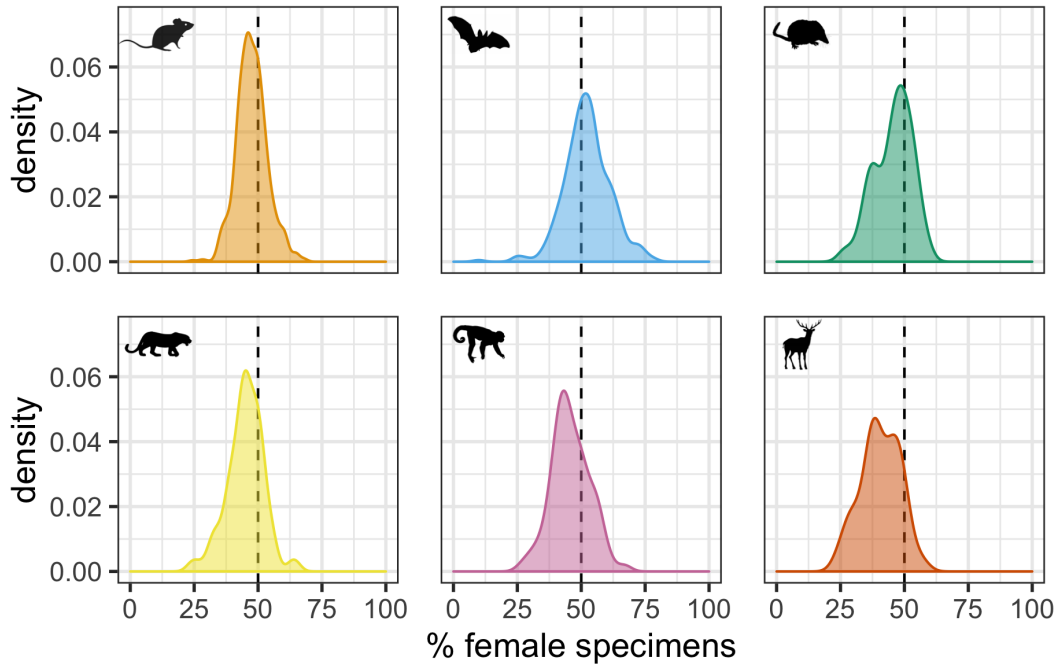


Figure 2: Kernel density plots showing the % female specimens in each species across the six largest orders of mammals (from left to right, top to bottom: Rodentia, Chiroptera, Soricomorpha, Carnivora, Primates, and Artiodactyla). Only species with at least 100 specimens are included. The dashed line represents 50% female specimens. Silhouettes are from PhyloPic.org contributed by Daniel Jaron (mouse), Yan Wong (bat), Becky Barnes (shrew), Lukasiniho (tiger), Sarah Werning (monkey), and Oscar Sanisidro (deer).

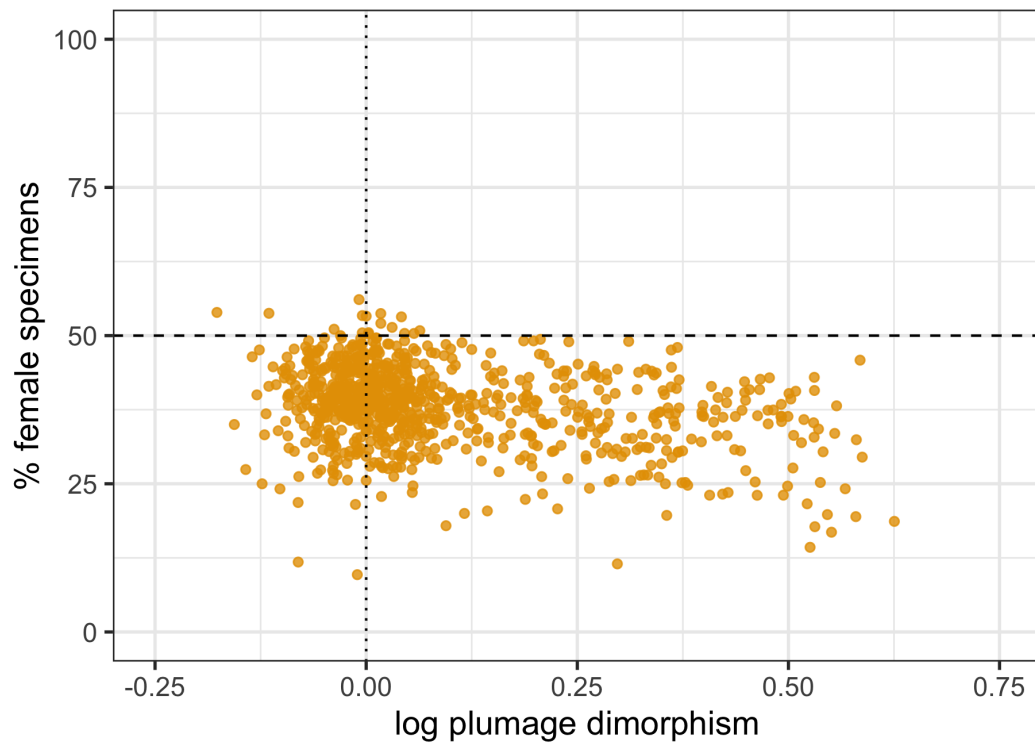


Figure 3: Relationship between the percentage of female specimens for each species and log plumage dimorphism scores in passerine birds. Only species with at least 100 specimens are included. The dashed line represents 50% female specimens; the dotted line is the point at which males and females have the same plumage colouration. Plumage dimorphism scores were calculated by dividing male plumage scores by female plumage scores (see Methods).

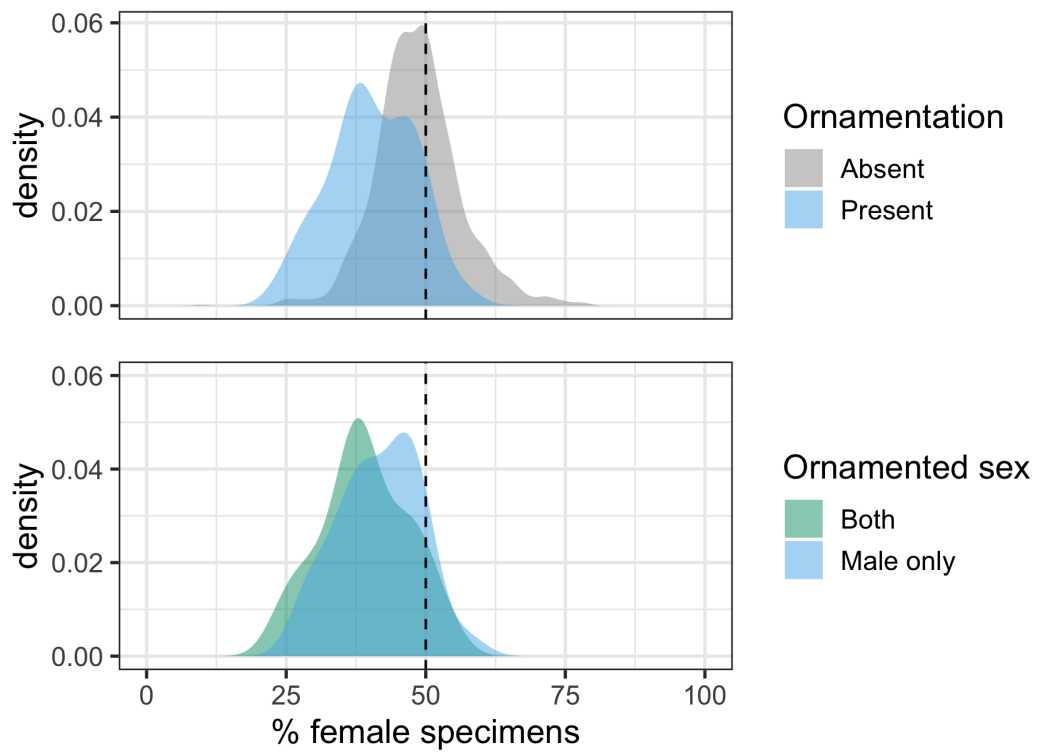


Figure 4: Kernel density plots comparing the % female specimens in each mammal species where ornaments, i.e. horns, tusks, antlers, manes etc., are present or absent (top panel), and when species have ornaments, whether these are found in both sexes or only males (bottom panel). Only species with at least 100 specimens are included. The dashed line represents 50% female specimens.

Table and figure legends

Table 1: Prominent uses of natural history specimens and how research outcomes may be influenced by sex biases.

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